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FACTORS CONTROLLING THE SECONDARY PRODUCTIVITY OF BENTHIC MACROINVERTEBRATES IN FRESHWATERS: A REVIEW

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Synopsis Among the groups of secondary producers, Chironomidae were the most productive, both in standing and running waters. A regression analysis was performed on the reported secondary productiondata for 39 herbivorous and detritivorous chironomid species in 37 standing waters. Annual mean biomass (B_a) was positively related to the maximum body weight of fourth-instar larvae (w_{4max}), P/B ratio was positively related to annual mean bottom temperature (T_{mean}) and inversely related to w_{4max}. Production (P) decreased with increasing mean water depth (z_{mean}). The latter relationship was also true for herbivorous and detritivorous zoobenthos. Secondary production of hervivores and detritivores including zooplankton and zoobenthos was ca. 10% of primary production in lakes. Zoobenthos production became comparable to that of zooplankton in lakes where primary production exceeded ca. 10000 kJ m^{-2} y^{-1}. Emerging biomass (E) of chironomids amounted to 0.1–1.6% of the sum of primary production and allochthonous organic matter. E/P value lay within 0.2–0.5 and tended to decrease with increasing P. Collection of emerging insects is recommended as a valid means of estimating species production. Annual chironomid production may be estimated by multiplying species annual emerging biomass by a factor of 2.8. The role of secondary producers in the nutrient cycling in a ecosystem is discussed.

Key Words: Chironomidae, Emergence, Eutrophication, Freshwater, Secondary production, Zoobenthos, Zooplankton

1. Introduction

MORGAN (1980) and DOWNING (1984) have consolidated the factors and various hypotheses considered to take part in the process of secondary production in freshwaters. The basic problem points have been summarized in these discourses. BRYLINSKY (1980), mainly on the basis of the IBP results, performed multivariate analyses on the factors which determine secondary production in freshwaters. Nevertheless, data on secondary production are few, and it has not been possible to amass sufficient data to analyze one taxonomic group (like Diptera) or

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or functional group (like herbivores and detrivores). For example, even looking at water temperature which probably most affects production, the P/B ratio has been shown to be related to water temperature in analyses including differing taxonomical groups, but within one taxonomical group the relationship has not been made clear (BANSE & MOSHER, 1980). It would be difficult to say that many of the hypotheses have been sufficiently verified.

The information on secondary production in freshwaters may, if anything, even be said to have been accumulated after IBP, and to see if we can consolidate things on secondary production and the factors controlling it at this point in time is thought to be meaningful. Here, first of all, in order to compare the estimated values of production obtained by various methods, an examination of the various production estimation processes will be done. Next, performing a comparison of the production by taxonomical group of zoobenthos considered to have a comparatively long life-span among secondary producers and whose distribution is considered to correspond to the long-term variations of the environment, the factors which control secondary production will be examined. In particular, an attempt will be made to consolidate the studies on the relationships between the eutrophication of waters and the ecosystem structure and secondary production.

Before getting into the main text, thanks are expressed to Mr. Takayuki HANAZATO and Mr. Kiyoshi SATAKE of the Environmental Biology Division of the National Institute for Environmental Studies from whom cooperation was received in literature surveys on the secondary production of zooplankton and lotic aquatic insects.

2. Methods of measurement and estimated values of secondary production (170)

2.1 Estimated values of production by various methods

The methods of measurement of secondary production can probably be classified in the following manner. With respect to those, like macrobenthos, whose individual body weight increment within a generation is comparatively large,

there are: 1) as methods to examine the growth and survival number over time, ① the removal summation method (WINBERG et al., 1971), ② the increment summation method (WINBERG et al., 1971), ③ the ALLEN curve method (ALLEN, 1951), ④ the instantaneous growth rate or growth speed method (JOHNSON & BRINKHURST, 1971), ⑤ the size-frequency method (HYNES & COLEMAN, 1968; HAMILTON, 1969; BENKE, 1979; MENZIE, 1980); 2) as methods to measure the losses in the final stage, ⑥ estimation of the pupal crop (BONOMI, 1962), ⑦ emergence quantification and the method of estimation from the P/E ratio (SPEIR & ANDERSON, 1974); and 3) as methods of

Table 1. A comparison of reported annual secondary production estimated by different methods
Values are relative percentages to one of the production values given in each reference.

Population	Methods[a]									Methods[b]			Reference
	RS	IS	AC	IGR	SF	PC	Es	Eb	R	ER	GIS	FAR	
Zoobenthos													
Simulated (weekly)[c]	100			96	122								Cushman *et al.* 1978
cohort (biweekly)[c]	100			84	127								
(monthly)[c]	100			91	129								
Stream mayfly	100		91	92	115								Waters & Crawfopd 1973
Stream mayfly	100		92	92	103								Giberson & Galloway 1984
Stream stonefly	100			102	95-107[d]								O' Hop *et al.* 1984
	100			89	80- 96[d]								
Lake chironomid		100		108									Jónsson 1985
Lake chironomid			100						22-96[e]				McLusky & McFarlane 1974; Maitland & Hudspith 1974
Lake chironomid		100							47-90[f]				McLusky & McFarlane 1974; Charles *et al.* 1974
Stream blackfly					100	18-28[g]							Speir & Anderson 1974
Stream chironomids	100					18-52[h]	3-45[h]						Present review
Chironomus plumosus				100		<58[i]							Potter & Learner 1974
Zooplankton													
Daphnia ambigua										104	100		Lei & Armitage 1980
Daphnia hyalina										22	100	84	Jones *et al.* 1979
Thermocyclops hyalinus										186	100		Burgis 1974; Rigler & Downing 1984

a Methods applied to the estimation of zoobenthos produdtion. RS: removal summation; IS: increment summation; AC: Allen curve; IGR: instantaneous growth rate; SF: size frequency; PC: pupal crop; Es: emergence in surface trap; Eb: emergence in bottom trap; R: estimation from respiration (McNeill & Lawton, 1971).

b Methods applied to the estimation of zooplankton production. ER: egg ratio (Edomondson, 1960); GIS: growth increment summation (Winberg, 1971); FAR: modified food assimilation rates (Jones *et al.*, 1979).

c Hypothetical sampling frequency

d A higher estimate is obatined by the Hamilton's method (1969) and a lower one by the Krueger & Martin's method (1980)

e Range of four determinations

f Range of three determinations

g Collection of pupal exuviae, range of eight determinations

h Nonpredatory chironomids. Production estimates obtained by RS, IS and IG are presumed to be identical (see Gillespie & Benke, 1979).

i Estimated from the fact that pupal crop per generation is less than annual maximum biomass, B_{max}.

estimation from other measurements, ⑧ the method of multiplying the mean biomass by the P/B ratio (WATERS, 1969), ⑨ the method of estimation from respiration (McNEILL & LAWTON, 1970; HUMPHREYS, 1979). Among these, methods ①~⑤ are used (171)
a lot. ① and ② are theoretically the same thing (GILLESPIE & BENKE, 1979). As well, with respect to those, like zooplankton, whose individual body weight increment within a generation is comparatively small, there are: ⑨ the egg ratio method (EDMONDSON, 1960), ⑩ the growth increment summation method (WINBERG, 1971), ⑪ the method of estimation from the feeding rate and assimilation efficiency (JONES et al., 1979). ⑨ was originally used in the production estimation of population groups, like rotifers, whose individual body weight increment within a generation is particularly small. It is not suited to the production estimation of population groups, like copepods, whose individual body weight increment within a generation is comparatively large. ⑩ is most often used.

In Table 1, the differences in estimated values or calculated values by various methods have been summarized. With calculation methods ①~⑤ which are used a lot on zoobenthos, in the case of population groups whose cohorts are separable, when the production was calculated based on the same data, the variation of the calculated values relative to ① is within 30% and comparatively small. By contrast, in the case of zooplankton, there is a disparity of approximately fourfold between methods ⑨ and ⑩. The fact that both the two methods used with zooplankton use the period of growth by indoor breeding as a parameter is probably the cause which makes the disparity between the estimated values large. Consequently, when comparing the production of zooplankton in different lakes, there is a need to take this point into consideration. Also, with ⑦, by virtue of multiplying the emergence by a certain factor (2.8 with chironomids, 4.5 with midges), the production can be estimated (see 2.2). The estimation by regression from respiration in ⑨ has large errors. Hereafter, unless otherwise indicated, the production of zoobenthos cited will be measured values based on methods ①~⑤.

The scatter in biomass estimations due to the sampling method also greatly affects the estimation of production. In the case of zooplankton, the movement and patchiness in the water mass, and in the case of zoobenthos the shifting in and out, become a problem, but in many of the secondary production studies this point has been omitted.

The fact that zoobenthos burrow deep into bottom matter has been observed in both running water (WILLIAMS & HYNES, 1974) and standing water (YAMAGISHI & FUKUHARA, 1970; FRANK, 1982). In Lake Kasumigaura, the maximum collection efficiency of an Ekman dredge was 55-65% with Chironomus plumosus of the family Chironomidae, 50-60% with Tokunagayusurika akamusi and 53-57% with Oligochaeta (IWAKUMA & YASUNO, 1981; IWAKUMA et al., 1984). Particularly in that the larger an organism in the final instar is, the deeper it burrows (SHIOZAWA & BARNES, 1977; IWAKUMA & YASUNO, 1981; FRANK, 1982), the biomass and production are prone to be underestimated.

2.2 Relationship between emergence and production of chironomids and method of estimation of production based on emergence

In Fig. 1 has been plotted the emergence/production ratio to production of chironomid insects in standing waters (see Table 2). Hereafter, the weight and production will all be expressed in dry weight. In the carnivorous suborder Tanypodinae, the scatter of the ratio is large (No. 5, 6, 9). In the four waters of Char Lake (No. 1), Eglwys Nunydd Reservoir (No. 6, 7), Lake Esrom (No. 14) and Lake Beloie (No. 15), a submerged type of emergence trap was used, while in the five other waters a surface-layer type of emergence trap was used. A number of comparisons have been done on the capture efficiency of the submerged type of funnel trap which is sunken until close to the bottom mud and the surface-layer type of box-shaped trap which is set on the water surface, in every one of which the recovery rate of the surface-layer type was better (KAJAK, 1958; MORGAN et al., 1963; KIMERLE & ANDERSON, 1974; POTTER & LEARNER, 1974). In Eglwys Nunydd

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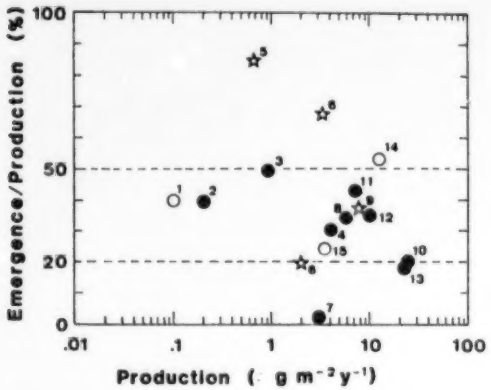

Fig. 1. Relation of annual emergence/production ratio to production for several chironomid species. ☆ : predatory chironomids (Tanypodinae) ; ○ : nonpredatory chironomids in a deep stratified lake ; ● : nonpredatory chironomids in a shallow lake.
1 : total of four species (Char L., WELCH, 1976) ; 2-5 : ***Polypedilum***, ***Tanypus***, ***Chironomus***, and ***Procladius***, respectively (wet-gravel pit, TITMUS & BADCOCK, 1980) ; 6-7 : ***Procladius*** and ***Glyptotendipes***, respectively (Eglwys Nunydd Reservoir, POTTER & LEARNER, 1974) ; ***Cricotopus*** (Hudson R. estuary, MENZIE, 1981) ; 9-10 : ***Anatopynia*** and ***Tanytarsus***, respectively (Root spring, TEAL, 1957) ; 11 : ***Glyptotendipes*** (sewage lagoon, KIMERLE & ANDERSON, 1971) ; 12-13 : ***Chironomus*** and ***Tokunagayusurika***, respectively (L. Kasumigaura, IWAKUMA *et al.*, 1984) ; 14 : ***Chironomus*** (L. Esrom, JÓNASSON, 1972) ; 15 : ***Chironomus*** (L. Beloje, BORUTSKI, 1939).

Reservoir, compared to the surface-layer type the catch of the submerged type was low (POTTER & LEARNER, 1974), with the emergence of Glyptotendipes in particular being extremely low (No. 7). If we exclude this and No. 5, 6, 9 of the Tanypodinae, the emergence/production ratio clusters in the 20-50% range (mean ± standard deviation, 35 ± 11%). In other words, 20-50% of the production of herbivorous or detrivorous chironomids are removed outside of the water system due to the emergence of adults. This ratio is seen to tend to decrease as production rises. One of the causes of this is thought to be that, because of the high density of larvae, the mortality prior to emergence is high. Also, another reason may be that, the higher the zoobenthos biomass of a lake is, the higher the predatory fish biomass becomes (HANSON & LEGGETT, 1982), and depending (172)

on the lake the predation pressure by fish at emergence gets as high as approximately 50% of the potential emergence (Lake Kasumigaura, No. 13, IWAKUMA & YASUNO, 1983).

From Fig. 1, with respect to chironomids in standing waters, it can be seen that if the emergence of adults is multiplied by a factor of 2~5, or 2.8 as a mean, the production can be estimated. In streams, the production of midges has been reported to be estimable by multiplying the emergence by a factor of 4~5 (SPEIR & ANDERSON, 1974). With other insects it is not clear, but the fact that the measurement of emergence serves as a means of rough production estimation is probably certain.

The measurement of emergence, when the bottom matter is gravel, rock or dense aquatic plants and such, is the only practical sampling method (DAVIES, 1984). In streams, even though the larval production may not have been examined, there are many examples where the emergence has been measured (ILLIES, 1971; MALICKY, 1976; CASPERS, 1983). When the distribution of larvae is nonuniform as in streams, the sample size could be large and there would be quantitativeness, while there is also the advantage that the identification of species by adults can be carried out. The trap used by ILLIES (1971) was a home greenhouse on the market with an area of indeed as much as 11 m^2. By means of this method the emergence by species of 144 species of chironomids from small streams in Germany (SIEBERT, 1980) and 114 species of chironomids from small streams in Austria (CASPERS, 1983) has been clarified, and the estimation of production has been made possible.

A similar method is the method of estimating by species the emergence of aquatic insects by recovering pupal exuviae drifting down a stream or floating on the surface of a lake (WILSON & BRIGHT, 1973; SPEIR & ANDERSON, 1974; IWAKUMA & YASUNO, 1983).

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3. Secondary production by species of zoobenthos

3.1 Range of secondary production of zoobenthos

Fig. 2 shows the annual production by species of zoobenthos by habitat, trophic level and taxonomical group. With respect to those for which no dry weight has been indicated in the literature, a conversion was done using 1 g dry weight = 6 g wet weight (WATERS, 1977). However, BORUTSKI et al. (1971), in comparing the production of chironomids in the Soviet Union, have, in order to make comparisons by wet weight, quintupled the dry weight value to estimate the wet weight, so in this case only it was deemed that 1 g dry weight = 5 g wet weight. The conversion between dry weight and thermal value was deemed to be 1 g dry weight = 5.5 kcal = 23.0 kJ for chironomids (CUMMINS & WUYCHECK, 1971), and 1 g dry weight = 5 kcal = 20.9 kJ for all other organisms (WATERS, 1977). With respect to those for which only the emergence (dry weight) has been indicated (ROSER, 1980; SIEBERT, 1980; CASPERS, 1983), the larval production has been estimated by multiplying it by a factor of 2.8 (see 2.2).

The lower limit of production shown in Fig. 2 has no meaning; what should be focused upon is how high a value is attained by each group. Both in standing waters and streams, the production of herbivores and detrivores is high, with the production of Chironomidae in particular being high being noteworthy.

These productions sometimes indicate particularly high values in a special environment such as a sewage treatment pond or in an experimental environment such as a recirculating waterway. For example, with chironomids the production of medium~large species is high in lakes and ponds, with a production of 41 $gm^{-2}y^{-1}$ being reported with Glyptotendipes paripes (Loch Levén, MAITLAND & HUDSPITH, 1974) and a maximum biomass of 65 gm^{-2} being reported with Polypedilum pavidus (Lake Rotongaio, FORSYTH & McCALLUM, 1983), but with G. barbipes in a sewage treatment pond a production of 92 $gm^{-2}y^{-1}$ has been reported (KIMERLE & ANDERSON, 1971). In streams the production of medium~small species is high,

with for example a production of 25 $g m^{-2} y^{-1}$ being reported with Cricotopus sylvestris in the Acorus zone of the River Thames (MACKEY, 1977) and a production of 34 $g m^{-2}$ in 37 days being reported with Orthocladius (Euorthocladius) calvus in a recirculating stream system (LADLE et al., 1985).

In high latitude regions, chironomids become the main secondary producer (Char Lake, 77°N, WELCH, 1976; Lake My, 66°N, LINDEGAARD & JÓNASSON, 1979). In the tropics, on the other hand, shellfish are dominant and high in production (Lake Chad, LÉVÊQUE & SAINT-JEAN, 1983), but in a highland lake chironomids sometimes predominate (Lake Nakuru, 0°S, elevation 1,759 m, VARESCHI & JACOBS, 1984). With Amphipoda, Gammarus appear in both standing waters and streams, and the production is high, 37 $g m^{-2} y^{-1}$ being reported in the former and 32 $g m^{-2} y^{-1}$ in the latter (MARCHANT, 1981).

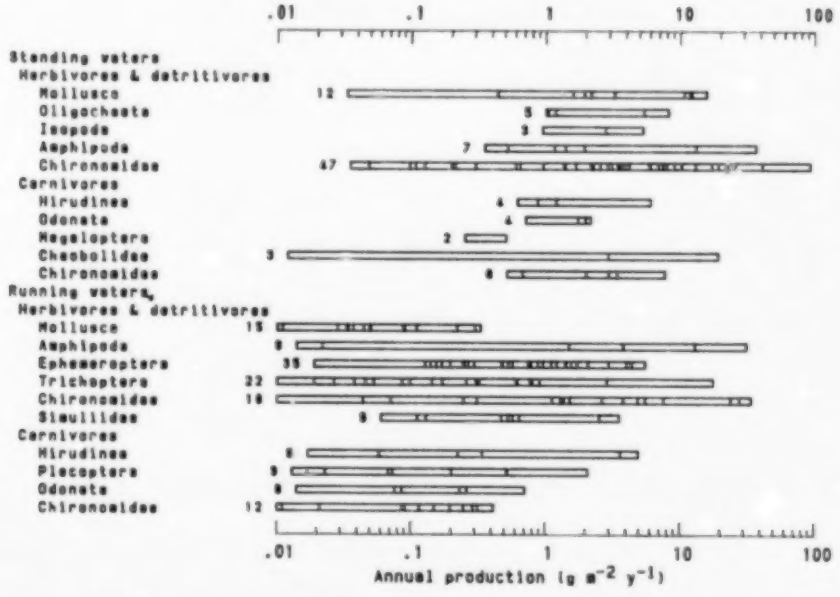

Fig. 2. Ranges of species-specific annual secondary production in different taxonomical groups. Numerals adjacent to the line indicate number of data.
Source :
WATERS (1977) : all taxa except for chironomids ; LÉVÊQUE & SAINT-JEAN (1983) : Mollusca ; JÓNASSON & THORHAUFE (1976), BONOMI & DI COLA (1980) : Oligochaeta ; MARCHANT (1980), LINDEMAN & MOMOT (1983) : Amphipoda ; DALL (1979), MURPHY & LEBANER (1982) : Hirudinea ; BENKE (1976) : Odonata ; IWAKUMA *et al.*, unpublished data : Chaoboridae ; WELTON *et al.* (1982), ZELINKA (1984) : Ephemeroptera ; BENKE & WALLACE (1980), BASS *et al.* (1982) MACFARLANE & WATERS (1982) : Trichoptera ; SMOCK *et al.* (1985) : Ephemeroptra, Odonata, Chironomidae ; NEVES (1979) : Ephemeroptera, Trichoptera, Plecoptera ; ROSER (1980), SIEBERT (1980), CASPERS (1983), LADLE *et al.* (1985) : lotic Chironomidae. A list of lentic Chironomidae is given in Table 2.

Studies on the production of Oligochaeta are few (JOHNSON & BRINKHURST, 1971a; FRANK, 1982; KASPRZAK, 1984). Instances where the production has been examined by species are even fewer (JONASSON & THORHAUGE, 1976; BONOMI & DI COLA, 1980). All are on lakes and ponds, and nothing is known about streams. In many (173) of the lakes and ponds it has been made clear that the biomass of Oligochaeta is high, which is thought to play an important role in terms of the circulation of matter, and studies on the production of this group are deemed to be necessary.

In streams the production of caddises and ephemera is also high. In experimental waterways the production of these zoobenthos becomes even higher (BASS et al., 1982; WELTON et al., 1982).

The production of carnivores is lower than the production of herbivores and detrivores. Among the carnivores the production of Chaoboridae is high, but their prey is zooplankton such as Daphnia (e.g., PASTOROK, 1980) and not zoobenthos, so a comparison with the production of herbivorous or detrivorous zoobenthos has no meaning. Carnivorous chironomids (Tanypodinae) prey mainly on other chironomids and Oligochaeta (MONAKOV, 1972; DUSOGE, 1980). The production of larvae of such carnivorous chironomids is approximately 20% of the production of primary consumer chironomids (WINBERG, 1972). Hirudinea too prey on zoobenthos such as Oligochaeta and chironomids (DALL, 1979). Erpobdella octoculata live in both streams (MURPHY & LEARNER, 1982) and lakes and ponds (DALL, 1979), and their production is high (5-6 $gm^{-2}y^{-1}$ in streams, 3 $gm^{-2}y^{-1}$ in lakes and ponds).

3.2 Secondary production of chironomids in standing waters and related factors

In Table 2 is a comparison of the production and related parameters by species of chironomids in standing waters where studies on secondary production among zoobenthos have been done comparatively extensively. The 37 waters examined, if we exclude Lake Nakuru in a tropical highland, Char Lake in the polar region (176) and Big Bear Lake (elevation 2,055 m) in a temperate highland, are all distributed

Table 2. A comparison of maximum body weight of 4th-instar larvae (w_{4max}), maximum density of 4th-instar larvae (N_{4max}), annual mean biomass (B_a), annual production (P), and annual emergence (E) for chironomid species in various standing waters. Morphometrical features and annual mean bottom water temperature are also shown in the table. An asterisc before the species name indicates that it is dominant in the study area.

Species	w_{4max} (mg)	N_{4max} (m^{-2})	B_a (mg m^{-2})	P (mg m^{-2})	E (mg m^{-2})	Locality	Lati-tude	Area (km^2)	Mean depth (m)	Annual mean temp. (°C)	Method & Refer-ence	
Pseudodiamesa arctica	1.3	23	23	35	28[a]	Lake Char, Canada	75°N	0.526	10.2	1	IGR[b]	1[c]
*Cricotopus ornatus	0.23	1000	20	107		Waldsea Lake, Canada	52°N	4.64	8.1	10	SF	2
*Cricotopus sylvestris	0.09	4634	277	5829	2000	Hudson R. estuary, USA	41°N		1	15	SF	3
*Heterotrissocladius oliveri	0.34	416	114	97		Lake Char, Canada	75°N	0.526	10.2	1	IGR	1
*Heterotrissocladius subpilosus	0.32	700		300		Langvatn, Norway	63°N	0.43	18.3	5	AC	4
Lauterborniа sp.	0.52	243	26	48	7[a]	Lake Char, Canada	75°N	0.526	10.2	1	IGR	1
Orthocladius lapponicus	0.22	740	53	125	64[a]	Lake Char, Canada	75°N	0.526	10.2	1	IGR	1
Trissocladius sp.	0.16	1558	102	199	57[a]	Lake Char, Canada	75°N	0.526	10.2	1	IGR	1
Tokunagayusurika akamusi	10.0	2770		3468		Lake Suwa, Japan	36°N	14.45	4.5	14	PC	5
Tokunagayusurika akamusi	10.0	6900	17900	22300	4000	Lake Kasumigaura, Japan	36°N	171	4.0	16	IS	6
Cladotanytarsus sp.	0.11		19	1389		Lake Norman, USA, (4m)	35°N	131.7	10.3	16	SF	7
Cladotanytarsus spp.	0.11	33200	317	3621		Lake Esrom, Denmark (2m)	56°N	17.3	12.3	9	IGR/IS	8
*Tanytarsus confusus	0.07		37	2883		Lake Norman, USA, (8m)	35°N	131.7	10.3	15	SF	9
*Tanytarsus confusus	0.07		50	6792		Lake Norman, USA, (4m)	35°N	131.7	10.3	16	SF	9
*Tanytarsus dives	0.44	57000		24900	5090	Root Spring, USA	42°N	0.000003	0.1	10	RS	10
*Tanytarsus gracilentus	0.3	20000	1966	19090		Lake Mývatn, Iceland	66°N	29.1	2.3	5	IS	11
*Tanytarsus holochlorus	0.22		582	5937		Upton Broad, UK	53°N	0.052	1.4	10	R	12
*Chironomus anthracinus	6.0	2000	1210	1350		Lake Varese, Italy	46°N	14.95	10.7	10	PC	13
*Chironomus anthracinus	6.0		1092	2258		Lake Memphremagog, Can.	45°N	43.7	6.9	13	IS	14
*Chironomus anthracinus	2.4	2968	10160	12885	6742	Lake Esrom, Denmark	56°N	17.3	12.3	7	IS	15
*Chironomus anthracinus	5.0	1930	6530	25700		Loch Leven, UK (mud)	56°N	13.31	3.9	10	IS	16
Chironomus decorus	1.6		33	2188		Lake Norman, USA	36°N	131.7	10.3	16	SF	7
Chironomus islandicus	4.5	12000	2340	7856		Lake Mývatn, Iceland	66°N	29.1	2.3	5	IS	11
*Chironomus plumosus	11.2		661			Livingstone Res., USA	31°N					17
Chironomus plumosus	7.0	400	2000			Tjeukemeer, Netherland	53°N	21	1.5	11	PB	18
*Chironomus plumosus	10.0	160				Fish pond, Yugoslavia	45°N			15		19
*Chironomus plumosus	12.0	2000				Lake Winnebago, USA	44°N	557	5	14		20
Chironomus plumosus	11.2	30	498			Lake Varese, Italy	46°N	14.95	10.7	10	PC	13
Chironomus plumosus	7.0	704	1362	2140		Alderfen Broad, UK	53°N	0.047	0.8	10	R	12
Chironomus plumosus	4.4		550	3510		Eglwys Nunydd Res., UK	52°N	1	3	12	IGR	21
*Chironomus plumosus	11.0	1052	1473	3534	870	Lake Beloie, USSR	57°N	0.27	4.15	6	RS	22
*Chironomus plumosus	8.0	1470		3850		Big Bear Lake, USA	34°N	12.1	7.38	12	?	23
Chironomus plumosus	5.7		714	4140	1280	wet-gravel pit, UK	52°N		2	15	SF	24
*Chironomus plumosus	12.0	1000		7328		Lake Suwa, Japan	36°N	14.45	4.1	14	PC	5
*Chironomus plumosus	14.0	1000	5409	8990		Federsee, West Germany	48°N	1.2	1.5	12	RS	25

Chironomus plumosus	11.8	1487	2175	10150	3600	Lake Kasumigaura, Japan	36°N	171	4	16	IS	6
*Chironomus plumosus	11.0		7160	21600		Bolshoie Medvechie, USSR	57°N				RS	26
*Chironomus plumosus	10.0		4660	22260		Lake Sevan, USSR	40°N			10	IGR	27
*Chironomus riparius	0.94	18600				Stephenson Pond, Canada	51°N	0.022		10		28
*Chironomus spp.	4.5	1446	8371	4149		Tundra pond, Alaska	71°N	0.0008	0.25	4	IS	29
Dicrotendipes pulsus	0.60	138	166	594		Loch Leven, UK (sand)	56°N	13.31	3.9	12	AC	30
Dicrotendipes pulsus	0.54	1050	382	2527		Lake Esrom, Denmark	56°N	17.3	12.3	9	IGR/IS	31
*Glyptotendipes barbipes	0.65		875	7434	3210	Sewage lagoon, Strat. 2	44°N	0.087		14	IGR	32
*Glyptotendipes barbipes	0.65		10860	92220		Sewage lagoon, Strat. 1	44°N	0.071	*	14	IGR	32
*Glyptotendipes pallens	3.5	2100				Tjeukemeer, Netherlands	53°N	21	1.5	11	PB	18
Glyptotendipes paripes	1.7	2210				Stephenson pond, Canada	51°N	0.022		10		28
Glyptotendipes paripes	3.7	1230	653	1660		Loch Leven, UK (mud)	56°N	13.31	3.9	10	IS	16
Glyptotendipes paripes	1.5		320	3080	85	Eglwys Nunydd Res., UK	53°N	1	2	13	IGR	21
Glyptotendipes paripes	1.9	1974	8136	40519		Loch Leven, UK (sand)	56°N	13.31	3.9	12	AC	30
*Leptochironomus deribae	0.53		510	17063		Lake Nakuru, Kenya	00°N	40	2.3	20	IGR	33
Polypedilum nubeculosum	0.80	316	143	641		Loch Leven, UK (mud)	56°N	13.31	3.9	10	IS	16
Polypedilum nubeculosum	0.8	144				Lake Dywity, Poland	53°N	0.18	3.5	11		34
Polypedilum nubeculosum	0.74		86	211	84	wet-gravel pit, UK	52°N		2	15	SF	24
*Polypedilum pavidus	0.6	133100				Lake Rotongaio, NZ	39° S	0.31	10.8	16		35
*Stictochironomus sp.	1.3	109	1042	10220		Loch Leven, UK(sand)	56°N	13.31	3.9	12	AC	30
*Tanypus punctipennis	1.5			3390		Lake Balaton, Hungary	47°N	596	3	12	R	36
*Tanypus punctipennis	1.5	1390	456			Neusiedlersee, Austria	48°N	175	1.0	11		37
Tanypus punctipennis	1.5		242	950	470	wet-gravel pit, UK	52°N		2	15	SF	24
*Tanypus stellatus	0.24	2774				Baldwin Lake, USA	38°N	7.6	3.3	18		38
*Tanypus stellatus	0.24	3500				Pickerel Slough, USA	50°N	0.065	0.8	13		39
Anatopynia, Pentaneura	0.58			7730	2900	Root spring, USA	42°N	0.000003	0.1	10	RS	10
Procladius sp.	0.50	4750	131			Neusiedlersee, Austria	48°N	175	1.0	11		37
Procladius bellus	0.50	490	1220	2940		Big Bear Lake, USA	34°N	12.1	7.38	12	?	23
Procladius choreus	0.54		156	673	571	wet-gravel pit, UK	52°N		2	15	SF	24
Procladius choreus	0.54		520	3410	379	Eglwys Nunydd Res., UK	52°N	1	3	12	IGR	21
Procladius rufovittatus	0.32		2415	2010	398	Eglwys Nunydd Res., UK	52°N	1	3	12	IGR	21
Procladius pectinatus	0.45	656	3420	517	303	Lake Esrom, Denmark	56°N	17.3	12.3	7	IS	15

a Emergence of one maturing generation among overlapping generations.

b Methods for estimating secondary production:
AC: Allen curve; IGR: instantaneous growth rate; IS: increment summation; PB: P/B ratio (5 is assumed); PC: pupal crop; R: respiration; RS: removal summation; SF: size frequency.

c References:
1: Welch, 1976; 2° Swanson & Hamner, 1983; 3: Menzie, 1981; 4: Aagaard, 1982; 5: Yanagishi & Fukuhara, 1971; 6: Iwakuma *et al.*, 1984; 7: Wilda, 1984; 8: Jónsson, 1985; 9: Wilda, 1984; 10: Teal, 1957; 11: Lindegaard & Jónasson, 1979; 12: Mason, 1977; 13: Bonomi, 1962; 14: Dermott *et al.*, 1977; 15: Jónasson, 1972; 16: Charles *et al.* 1974; 17: McCullough & Jackson, 1985; 18: Beattie, 1982; 19: Jankovic, 1971; 20: Hilsenhoff, 1967; 21: Potter & Learner, 1974; 22: Borutski, 1939; 23: Siegfried, 1984; 24: Titmus & Badcock, 1980; 25: Frank, 1982; 26: Yablonskaya, 1947 (after Winberg, 1971); 27: Ostrovskii, 1982; 28: Rasmussen, 1984; 29: Butler, 1982; 30: Maitland & Hudspith, 1974; 31: Jónsson, 1985; 32: Kimerle & Anderson 1971; 33: Vareschi & Jacobs, 1984; 34: Wielgoss, 1984; 35: Forsyth & McCallum, 1983; 36: Oláh, 1976, Biró, 1984; 37: Schiemer, 1979; 38: Parkin & Stahl, 1981; 39: Heuschele, 1969

between 31～66°N below an elevation of 800 m. The maximum weight of the larvae shows a disparity of some hundredfold plus from the smallest Cricotopus sylvestris to the largest Chironomus plumosus. The production of larvae is shown to be the highest with medium-sized Glyptotendipes. The production and emergence have been shown separately. Those cases where the production was estimated assuming a P/B ratio (BEATTIE, 1982) have been excluded.

Table 3 shows the simple correlation coefficients among these parameters. The maximum weight (w_{4max}) of the larvae indicated a positive correlation with the annual mean biomass (B_a) ($p < 0.05$). While the secondary production (P) was correlated with B_a and emergence (E), a higher correlation was shown with the latter, suggesting the propriety of estimating P based on E (see 2.2). While the P/B ratio indicated a positive correlation with the annual mean water temperature (T_{mean}) ($p < 0.01$), since T_{mean} declines as latitude increases ($p < 0.01$), the P/B ratio indicated a negative correlation with latitude ($p < 0.01$).

JOHNSON & BRINKHURST (1971a) found that the P/B ratio of zoobenthos in

Table 3. Matrix of simple correlation coefficients among parameters of herbivorous chironomid production and environmental factors Symbols are the same as in Table 2 except for the following. z_{mean}: mean depth; T_{mean}: annual mean bottom temperature.

No. Variable	1 w_{4max}	2 N_{4max}	3 B_a	4 P	5 E	6 P/B	7 Area	8 z_{mean}	9 T_{mean}
2 N_{4max}	−.214	.							
	(42)								
3 B_a	.346*	.036	.						
	(41)	(28)							
4 P	.011	.360*	.639**	.					
	(46)	(30)	(40)						
5 E	.253	.468	.709**	.847**	.				
	(15)	(10)	(14)	(15)					
6 P/B ratio	−.293	.424*	−.229	−.067	.056	.			
	(40)	(25)	(40)	(40)	(14)				
7 Area	.201	−.077	.158	−.053	.378	.603**	.		
	(51)	(40)	(37)	(40)	(11)	(34)			
8 z_{mean}	−.189	.107	−.148	−.329*	−.037	.267	−.079	.	
	(51)	(39)	(39)	(42)	(14)	(36)	(47)		
9 T_{mean}	.170	.186	.096	.202	.316	.430**	.265	.340*	.
	(57)	(42)	(42)	(45)	(15)	(39)	(51)	(51)	
10 Latitude	−.285*	−.137	−.074	−.195	−.599*	−.526**	−.253	.197	−.873**
	(59)	(42)	(44)	(46)	(15)	(40)	(51)	(51)	(57)

* Significant at 0.05 probability level
** Significant at 0.01 probability level
(n) Number of data set

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Lake Ontario is proportional to approximately the square of the annual mean temperature (n=15). BANSE & MOSHER (1980), on the other hand, gathered secondary production data on 48 species of invertebrates from literature and analyzed the relationship with various factors. While they showed that the smaller the size of a secondary producer is, the higher the P/B ratio becomes, they were not able to obtain a significant regression between the P/B ratio and water temperature. Among these organisms, chironomids were included in 11 cases, while in the analysis involving temperature six cases were included. Upon examining the correlations in terms of the logarithm of each variable in Table 3, the P/B ratio indicated a significant correlation with both w_{4max} and T_{mean} ($r=-.508$, $n=40$, $p<0.01$ and $r=.494$, $n=39$, $p<0.01$). Consequently, with respect to chironomids, the conclusions derived separately by JOHNSON & BRINKHURST (1971a) and BANSE & MOSHER (1980) were both confirmed.

In lake basin configurations, the results obtained showed that the shallower the mean water depth (z_{mean}) gets, the more P increases ($p<0.05$), but with B_a no significant relationship whatsoever could be found. Up to now the relationship between the biomass of zoobenthos and water depth has been examined by many researchers, but no correlation has been obtained, for example, from the data on 158 lakes and ponds (according to HAYES, 1957, JOHNSON, 1974). HARGRAVE (1973) showed that the deeper the mixed water depth of a water mass is, the more becomes the decomposed quantity of primary products in the water and the less becomes the quantity which reaches the bottom mud surface layer and decomposes there. This is thought to be equivalent to the fact that the deeper the mixed water depth is, the less becomes the quantity of food supplied to zoobenthos, which agrees with the results of analysis of the secondary production (177) of chironomids shown here. From the studies done thus far, a negative correlation between fish yield and the mean water depth of lakes has come to be made clear (MATUSZEK, 1978; HANSON & LEGGETT, 1982). Nevertheless, on the relationship of

the secondary production of zoobenthos and water depth, while its possibility had been pointed out (JOHNSON, 1974; DOWNING, 1984), no significant relationship had been obtained (BRYLINSKY, 1980).

JOHNSON (1974), in analyzing the relationship between the production of zoobenthos and the inorganic environment, used a "production index" (P/B ratio estimated from biomass x water temperature) in lieu of secondary production. Pointing out that besides water depth the lake area also is a factor which has an effect on secondary production, he made it clear that in alpine lakes the "production index" and lake area indicate a negative correlation. This is said to be because, as the lake area increases, the proportion occupied by the profundal zone increases, and the contribution of the littoral where primary production is high and the supply of allochthonous organic matter is abundant, decreases. In the present analysis, no relationship whatsoever could be found between the area of a water surface and the secondary production of chironomids, but rather a positive correlation was seen with the P/B ratio ($p < 0.01$, Table 3). The meaning of this result is unclear, and an examination hereafter would seem to be necessary.

While herbivorous chironomids live on the bottom surface and use a certain area (denoted A_r) as their feeding range, feeding on sedimentary organic matter, this A_r is thought to be proportional to the square of the body length. Consequently, the maximum number of individuals that can exist in a fixed area of bottom matter is thought to be proportional to the -square of the body length, that is, -2/3 power of the body weight. Also, the maximum biomass that can exist in a fixed area of bottom matter is thought to be proportional to the body length, that is, 1/3 power of the body weight. No significant regression has been obtained between the maximum number of fourth-instar larvae (N_{4max}) and w_{4max}. The regression coefficient of log B_a to log w_{4max} was 0.75 ± 0.29 (95% confidence limits) and greater than 1/3. Among the reasons for this, in large species like

Tokunagayusurika akamusi and Chironomus plumosus, there are those whose activity in the fourth instar becomes inactive due to dormancy and such (YAMAGISHI & FUKUHARA, 1970; FISCHER, 1974), and this can be thought to diminish the interference action between individuals.

DAVIES (1980) found that the more a lake is experimentally eutrophied, the more the emergence of large dipterous insects increases (see 4.2). Also, JÓNASSON (1972) has pointed out that large chironomids stir up the layer of low oxidation-reduction potential in the bottom mud surface layer and enable the subsistence conditions in eutrophic lakes to become favourable. As yet, however, the relationship between size and secondary production, apart from the P/B ratio, is unclear.

3.3 Other factors related to secondary production

The factors which limit the distribution of zoobenthos, such as the dissolved oxygen condition in eutrophic lakes, in effect also control secondary production.

Among chironomids of the genus Chironomus, within the same species fourth-instar larvae are stronger in resistance to low oxygen than third-instar ones (C. plumosus, FRANK, 1983), while C. plumosus are stronger in resistance than C. anthracinus. For example, the LT_{50} of fourth-instar larvae at 4° C is 205 days for the former whereas it is 100 days for the latter (NAGELL & LANDAHL, 1978). In reality, however, what is distributed in the profundal zone which becomes oxygenless in lakes and ponds are instead C. anthracinus (BONOMI, 1962; JÓNASSON, 1972), while C. plumosus live in the littoral to sublittoral where the dissolved oxygen is above 50% saturation (BONOMI, 1962; NEUBERT & FRANK, 1980), so their distribution does not necessarily agree with low-oxygen aptitude.

Not only the dissolved oxygen condition but the utilizability of feed as well is a factor controlling distribution. Within the same lake, C. plumosus are deemed to feed on fresh phytoplankton sediments while C. anthracinus feed on

detritus (JOHNSON, 1985). Aside from this, however, the feeding habit of C. plumosus has been reported to differ variously depending on the environment, from phytobenthos (KAJAK & WARDA, 1968; JOHNSON, 1985) to bacteria and protozoa (ZIĘBA, 1984) and aquatic macrophyte remains (RASMUSSEN, 1982), etc. The relationship between secondary production and feeding conditions, that is, primary production, shall be discussed in 4.1.

4. Environmental pollution and secondary production - eutrophication -

4.1 Relationship between eutrophic level of lakes and ponds and secondary production

If we compare lakes of different trophic levels, it is natural that the higher the trophic level of a lake is, the higher would be the biomass of phytoplankton which is a primary producer, but the biomass of secondary producers such as zooplankton and zoobenthos also increases (BAYS & CRISMAN, 1983; YASUNO et al., 1983; HANSON & PETERS, 1984). The secondary production of zooplankton communities in eutrophic lakes is in the range of 20-89 $gm^{-2}y^{-1}$ with herbivores and 2-20 $gm^{-2}y^{-1}$ with carnivores (MORGAN, 1980). In comparison with the secondary production of these zooplankton, the secondary production of the zoobenthos in Fig. 1 is roughly of the same order.

The biomass and production of zooplankton and zoobenthos often get linked to the quantity of feed, that is, the biomass and production of phytoplankton. The correlation between primary and secondary producers becomes clearer by making the comparison in terms of production rather than biomass (BRYLINSKY, 1980). While the secondary production of herbivorous zooplankton and zoobenthos each indicates a correlation with the primary production of phytoplankton, zooplankton indicates a higher correlation (BRYLINSKY, 1980).

Among the primary producers, besides phytoplankton, are included aquatic macrophytes, attached algae and phytobenthos as well, which also become utilizable feed for zoobenthos (RASMUSSEN, 1982; KAJAK & WARDA, 1968). (178)

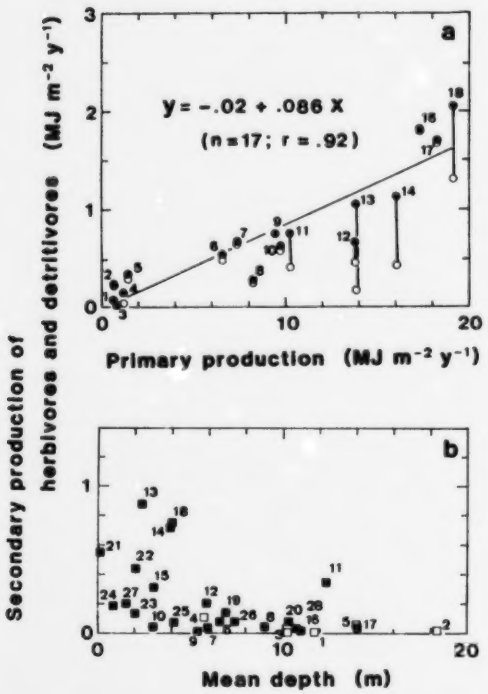
a
y = -.02 + .086 X
(n = 17; r = .92)
Secondary production of herbivores and detritivores (MJ m⁻² y⁻¹)
Primary production (MJ m⁻² y⁻¹)
b
Mean depth (m)

Fig. 3. a : Relation of annual secondary production of herbivores and detritivores (zooplankton + zoobenthos) to annual primary production (phytoplankton + phytobenthos + aquatic macrophytes)
○ : zooplankton ; ● : zooplankton + zoobenthos
Regression was calculated for production of zooplankton + zoobenthos.
b : Relation of annual secondary production of herbivorous and detritivorous zoobenthos to mean depth of lake
□ : oligotrophic lake ; ■ : meso- or eutrophic lake
Numerals indicate lakes in the order of increasing primary productivity.
1 : Krivoe (ALIMOV *et al.* 1972) ; 2 : Langvatn (AAGAARD, 1982) ; 3 : Char (KALFF & WELCH, 1974 ; WELCH 1976) ; 4 : Mirror (LIKENS, 1985) ; 5 : Pääjärvi (SARVALA, 1981) ; 6 : Krasnoe (WINBERG, 1972) ; 7 : Drivyati(WINBERG, 1972) ; 8 : Naroch (WINBERG, 1972) ; 9 : Myastro (WINBERG *et al.*, 1972) ; 10 : Batorin (WINBERG *et al.*, 1972) ; 11 : Esrom(JÓNASSON, 1972, 1977) ; 12 : Sniardwy (KAJAK *et al.*, 1972) ; 13 : Mývatn-south basin (JÓNASSON, 1979) ; 14 : Loch Leven (MORGAN *et al.*, 1972 ; CHARLES *et al.*, 1974) ; 15 : Balaton (BIRÓ, 1984) ; 16 : Mikołajskie (KAJAK *et al.*, 1972) ; 17 : Taltowisko (KAJAK *et al.*, 1972) ; 18 : Kasumigaura (IWAKUMA *et al.*, 1984 ; TAKAMURA *et al.*, 1984 ; HANAZATO & YASUNO, 1985) ; 19 : Memphremagog (DERMOTT *et al.*, 1977) ; 20 : Norman (Wilda, 1984) ; 21 : Root Spring (TEAL, 1957) ; 22 : Eglwys Nunydd (POTTER & LEARNER, 1974) ; 23 : wet-gravel pit (TITMUS & BADCOCK, 1980) ; 24 : Alderfen Broad (MASON, 1977) ; 25 : Beloie (BORUTSKI, 1939) ; 26 : Big Bear (SIEGFRIED, 1984) ; 27 : Federsee (FRANK, 1982) ; 28 : Varese (BONOMI, 1962)

WINBERG (1972), from investigations of seven lakes and two reservoirs in the Soviet Union, showed that ① the feeding level of herbivorous zooplankton is closely related to the primary production of phytoplankton and is approximately

31-51% of the latter, and ② the secondary production of herbivorous zooplankton and zoobenthos turns out to be approximately 10% of the primary production (phytoplankton + phytobenthos + aquatic macrophytes).

Fig. 3a shows the relationship between the annual primary production of lakes (phytoplankton + phytobenthos + aquatic macrophytes) and the annual secondary production of herbivores (zooplankton + zoobenthos) (n=18). Where the primary production had been expressed in carbon value, it was converted to thermal value using 1 gC = 6.96 kcal = 29.1 kJ (CUMMINS & WUYCHECK, 1971). For the production of zoobenthos, in the case of lakes that thermally stratify, the value in the profundal zone has been used.

In Lake Mikolajskie, Lake Taltowisko and Lake Kasumigaura where the primary production is highest, secondary production sometimes gets higher than 10% of the primary production (Fig. 3a). The secondary production of zoobenthos is high in deep lakes, but when the water depth is less than 10 m it becomes low (Fig. 3b).

While PEDERSON et al. (1976) claimed that the higher the production of phytoplankton gets, the smaller becomes the energy transformation efficiency to zooplankton (zooplankton production/phytoplankton production) (n=11), in the results of an analysis done by BRYLINSKY (1980) on a larger number of lakes and ponds (n=27), the scatter in the regions of high production of phytoplankton was large and this tendency was not clear. According to Fig. 3a, in regions where the annual primary production is higher than approximately 10,000 $kJ\,m^{-2}y^{-1}$ (340 $gC\,m^{-2}y^{-1}$), a tendency for the annual secondary production of zoobenthos to be high can be seen, and correlatively the importance among secondary producers seems to increase.

Table 4 shows a comparison of the annual emergence of chironomids and the annual gross primary production. The emergence diverges widely between 0.1-4.6% of the annual gross primary production depending on the waters.

Table 4. Ratio of emerging chironomid biomass (*E*) to gross primary production (*PP*) and that to *PP* plus allochthonous matter (*AM*) in several standing waters (unit: kJ $m^{-2}y^{-1}$)
Emerging biomass was converted to energy value by multiplying by 22.0 kJ g^{-1} given by KIMERLE & ANDERSON (1971).

Waters	*PP*	*AM*	*E*	*E*/*PP* (%)	*E*/(*PP*+*AM*) (%)	Reference
Char	879	-[a]	3.3	0.4	(0.4)[d]	WELCH 1976; KALFF & WELCH 1974
Pääjärvi	1454	2466	5	0.3	0.1	SARVALA 1981
ELA lakes	1455	-	9[c]	0.6	(0.6)	DAVIES 1980
Root Spring	2970	9840	138	4.6	1.1	TEAL, 1957
Esrom	10250	-	167	1.6	(1.6)	JÓNASSON 1972, 1984
Kasumigaura	19110	-	167	0.9	(0.9)	IWAKUMA *et al.* 1984; TAKAMURA *et al.* 1984
Lago Pond	30930	-	(240)	0.8	(0.8)	WELCH 1973
Sewage lagoon	89500	6400	66	0.1	0.1	KIMERLE & ANDERSON 1971

a Data not available
b Estimated value
c Diptera

Table 5. Relation of annual secondary production of nonpredatory zoobenthos to annual sedimentation in several lakes (unit: kJ $m^{-2}y^{-1}$)

Lake	Sedimentation, *S*	Zoobenthos production, *P*	*P*/*S* (%)	Reference
Pääjärvi	182	70	38.5	SARVALA 1981
Mirror	1150	110	9.6	LIKENS 1985
Ontario, Conway	1649	264	16.0	JOHNSON & BRINKHURST 1971b
Ontario, Glenora	1926	674	35.0	JOHNSON & BRINKHURST 1971b
Esrom	3485	347	10.0	JÓNASSON 1972; LASTEIN 1976
Mikołajskie	4605	169	3.7	ŁAWACZ 1969; KAJAK *et al.* 1972
Kasumigaura	9030	746[a]	8.3	IWAKUMA *et al.* 1984; FUKUSHIMA *et al.* 1984

a Chironomidae

In these waters, however, are also included those which, by virtue of being oligotrophic (Lake Pääjärvi, SARVALA, 1981) or being small in area (Root Spring, TEAL, 1957), have a high ratio of allochthonous organic matter to primary production. The annual emergence of chironomids is equivalent to 0.1-1.6% of the sum of the gross primary production and allochthonous organic matter (Table 4).

In the pathways of primary producers and secondary producers are also pathways which include bacteria. In general if a lake is eutrophic the amount of bacteria also gets abundant (WETZEL, 1983), and the volume which shifts from the primary products of phytoplankton to the production of bacteria is likewise thought to increase. Planktonic bacteria play an important role as feed for zooplankton (PETERSON et al., 1978; PEDROS-ALIO & BROCK, 1983), but in deep lakes, because their biomass is high in the epilimnion and low in the hypolimnion

(WETZEL, 1983), their importance as food for zoobenthos is thought to diminish. While the feed of Oligochaeta, however, is bacteria in bottom matter (WAVRE & BRINKHURST, 1971), these bacteria probably differ in origin from planktonic ones.

Among zoobenthos, the suborder Tanypodinae deemed to be typical carnivores feed on algae as well depending on the species (TEAL, 1957). On the other hand, the herbivorous chironomid Cricotopus sylvestris, under experimental conditions, is able to feed on the zooplankter Bosmina (MONAKOV, 1972). From the fact that in this way the feeding habits change according to feeding conditions and the faculties of herbivores and carnivores are not something fixed, and that the pathway of primary production → secondary production is not simple, the interpretation of energy transformation efficiency between trophic levels is difficult.

It would be thought appropriate that the energy transformation efficiency from the feed of herbivorous or detrivorous zoobenthos be based on the sedimentation volume. However, there are few lakes on which data extend to sedimentation in addition to primary production and secondary production, all that there are being shown in Table 5. In sedimentation measurement, there is a need to correct the upwelling volume of bottom mud in terms of Fe, Al, Pb (HAMILTON-TAYLOR et al., 1984) and Ti and organic matter content (FUKUSHIMA et al., 1984). (180)
The annual secondary production of herbivorous or detrivorous zoobenthos/annual sedimentation ratio in these lakes, excluding oligotrophic Lake Pääjärvi (38%) and the Glenora site of eutrophic Lake Ontario (35%), lies between 4-16%.

4.2 Eutrophication experiments by adding nutrient salts to lakes and ponds

In the Experimental Lakes Area (= ELA) in Canada (SCHINDLER & FEE, 1974; DAVIES, 1980), Great Central Lake in Canada (LEBRASSEUR et al., 1978) and Lake Lang in Norway (AAGAARD, 1982), large-scale nutrient salt-adding experiments have been done. In the experiments aimed at the improvement of fish production in oligotrophic lakes, increases were seen in the primary production of phytoplankton and the biomass of zooplankton during fertilization. Moreover with respect to zoobenthos the following results have been obtained.

In oligotrophic lakes, virtually no zoobenthos are in the profundal zone, but if eutrophication is artificially contrived by adding nitrogen and phosphorus (DAVIES, 1980; AAGAARD, 1982), while it would be natural for primary production to increase, ① the emerging number and emerging biomass per year of dipteran insects (particularly chironomids) increase (DAVIES, 1980), ② the body weight of the emerging adults gets heavier, that is, more large species start appearing (DAVIES, 1980), and ③ the larval biomass increases, but if the nutrient addition is stopped and the primary production per year of the lake decreases, once again the chironomid larval biomass will decrease (AAGAARD, 1982).

4.3 Eutrophication experiments in experimental ponds or fishponds

HALL et al. (1970) established three levels of nutrient salt level in experimental ponds at Cornell University and examined primary production and secondary production. The primary production of phytoplankton and the secondary production of zooplankton in every case increased in the pond with a high amount of nutrient salt added. The secondary production of zoobenthos, however, showed large variations within the same treatment sector, and the difference between ponds due to the amount of nutrient salt added was not clear. Neither did the emergence of chironomids by pond necessarily correspond to the amount of nutrient salt added.

In eutrophied fishponds (ZIĘBA, 1971), because the production of zoobenthos is high to start with, the increase in secondary production of zoobenthos due to nutrient salt addition was not necessarily clear.

Whenever a pond or reservoir is newly formed, a change can be seen in the biological communities therein, and with chironomids in particular the replacement of species is pronounced (DRIVER, 1977; SIKOLOWA, 1977). In eutrophication experiments in natural lakes and ponds, the relationship between primary production and the secondary production of zoobenthos was clear, but in small experimental ponds, because the benthic fauna undergoes change, this relationship is thought not to have necessarily appeared clearly.

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4.4 Supply of primary products to secondary producers

As stated previously in 3.1, between the secondary producers called zooplankton and zoobenthos, it has been suggested that there is competition surrounding primary producers which constitute their feed. These two, however, often lag each other seasonally in dominance period. In temperate Lake Mikolajskie, the peak of gross primary production of phytoplankton is high in summer, and the production of bacteria and secondary production of zooplankton also roughly coincides with this (KAJAK, 1978). The rate of supply of sinking materials, on the other hand, is high in the spring and autumn (LAWACZ, 1969), and the peak of production of herbivorous or detrivorous zoobenthos coincides with this (KAJAK, 1978).

In this way, in eutrophic lakes in the temperate zone, which stratify when the autumn overturn occurs, the growth of larvae which until then had been inhibited under the anoxic conditions of the hypolimnion accelerates at once due to the simultaneous supply of and oxygen. Chironomus anthracinus which can survive for a long period in low oxygen is a typical zoobenthic organism of the profundal zone of these lakes (Lake Esrom, JÓNASSON, 1972; Lake Memphremagog, DERMOTT et al., 1977). The syntonic relationship between the supply of primary products and the secondary production of zoobenthos has been seen elsewhere in Loch Leven as well (BINDLOSS, 1974; CHARLES et al., 1974).

In shallow eutrophic Lake Kasumigaura, the seasonal variation in production structure resembles the aforementioned lakes with respect to zooplankton and phytoplankton but differs greatly with regard to zoobenthos.

In Lake Kasumigaura during the four-month period of June~September, Myxophyceae such as Microcystis are dominant among phytoplankton, with the gross primary production during this period corresponding to 40% of that for the year (TAKAMURA et al., 1984). Among zooplankton, Cladocera such as Bosmina are dominant, with the secondary production during the four-month period of summer

corresponding to 82% of that for the year (HANAZATO & YASUNO, 1985). Because Myxophyceae have a slow sedimentation rate while Cladocera have a rapid feeding rate at high temperature, the circulation of matter involving [phytoplankton → zooplankton → nutrient salt recycling] or [phytoplankton → bacteria → zooplankton → nutrient salt recycling] takes place for the most part in water (YASUNO et al., 1984). The amount of sinking materials is low in summer but abounds in two peaks in the spring and autumn when Diatomaceae are dominant (FUKUSHIMA et al., 1984). Approximately 90% of the zoobenthos biomass are chironomids, with univoltine Tokunagayusurika akamusi being dominant. Hatched larvae of T. akamusi grow rapidly in the low-temperature period of December ~ March and their secondary production rate is high, but they lie dormant in the bottom mud in summer. Chironomus plumosus with the next highest biomass undergo three generations a year, but are not as adaptable to low temperature as T. akamusi, growing mainly in the spring and autumn, and becoming final-instar larvae in the high water-temperature period of summer with the growth stopping (IWAKUMA et al., 1984). The production of C. plumosus in spring coincides with the peak of sedimentation. (181) The peak of production of T. akamusi, however, lags both the primary production and sedimentation. In this way between the two principal secondary producers, a seasonally-separated production structure can be seen involving cladoceran zooplankton of summer, T. akamusi of winter and C. plumosus of the other seasons.

4.5 Negative feedback by secondary producers to eutrophication

In Lake Kasumigaura, in winter the secondary production rate of zoobenthos was seen to equal the primary production rate (IWAKUMA et al., 1984) and exceed the rate of supply of sinking materials (FUKUSHIMA et al., 1984). These sedimentary organic materials, when not eaten by zoobenthos, are preserved in the bottom mud without being decomposed in winter because of low temperature, and are supposed to be decomposed the following spring when the water temperature rises and the nutrient salts would recycle back into the water. T. akamusi takes in this

sedimental organic matter in winter when the water temperature is low, part of which is turned inorganic during the winter by respiration and excretion while the remaining products are preserved as entosomatic matter in the bottom mud until autumn. T. akamusi, by this sort of process, reduces the nutrient salt supply during the period of high phytoplanktonic activity of spring~summer and thereby gives a negative feedback to the eutrophication of the lake.

In many lakes and ponds, the production of zoobenthos in winter has not been examined in detail. This is due to the fact that in general zoobenthos diminish in activity at low temperature (JOHNSON & BRINKHURST, 1971a; WINBERG, 1971) and that freezing makes the collection of zoobenthos difficult.

HARGRAVE (1973) showed that, in eutrophic Lake Esrom, the oxygen consumption in the bottom mud surface layer exceeds the oxygen supply by primary production in winter. Even under low temperature it means decomposition had proceeded for certain, but as to how the zoobenthos through production activity participates in this process is not clear.

As the effects of secondary producers on the circulation of matter in water mass ecosystems, besides the aforementioned ① inhibition of the recycling of matter due to a time lag between primary production and secondary production, mention can be made of ② the accumulation of organic matter (see 4.1), ③ the recycling of matter that accompanies feeding activity (see 4.4), ④ the delivery of organic matter to higher-order predators (see 2.2), ⑤ the removal of organic matter accompanying emergence (see 2.2).

5. Future topics

With respect to secondary production, the topics which have thus far not been studied that much would include ① Oligochaeta and microbenthos as target species, ② in terms of content, seasonal production relationships and organic matter decomposition by secondary producers in winter, ③ chemical substances and heavy metals in terms of pollutants, ④ experimental ecosystems in terms of place, and ⑤ in terms of methodology, emergence quantification by species based on adults.

As a secondary producer which should be studied, among the ones on which there are few research cases in spite of the biomass being high can be mentioned Oligochaeta among macrobenthos. As well, studies on the secondary production of microbenthos, despite the fact that its production is claimed to amount to as much as 15-50% of the production of all zoobenthos depending on the lake (KAJAK & RYBAK, 1966), are far fewer than secondary production studies on macrobenthos.

Studies on secondary production in winter are few. There is a need to clarify the decomposition of bottom mud organic matter that accompanies the feeding activity of secondary producers and the biological production structure and function by season.

With respect to environmental pollution effects other than eutrophication, there are many studies of the accumulation of chemical substances and heavy metals in zoobenthos and such as monitoring organisms, but in terms of studies related to secondary production, an examination on the removability of pollutants from bottom matter by the emergence of aquatic insects is about the extent of it (MENZIE, 1980; LARSSON, 1984). Research in this area is to be hoped for. Thermal pollution increases the secondary production of zoobenthos (RASMUSSEN, 1982).

As experimental ecosystems which can be used in secondary production research, there are experimental waterways, experimental ponds, isolated water masses and such. In standing waters, isolated water masses encompassing natural lacustrine ecosystems exactly as they are and far more stable than experimental ponds, are being used in estimating the effects of toxic pollutants on ecosystems (LUNDGREN, 1985) or analyzing the ecosystem structure (LYNCH, 1979) and such. Many of these studies are being done at the level of the zooplankton and phytoplankton structure or primary production, and few are on secondary production (KAJAK & RYBAK, 1979). For the verification of a number of hypotheses derived from studies of lacustrine ecosystems, for example the competitive relationship between zooplankton and zoobenthos groups or the relationship between lake basin

configurations and secondary production, isolated water masses will no doubt serve as an effective means.

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